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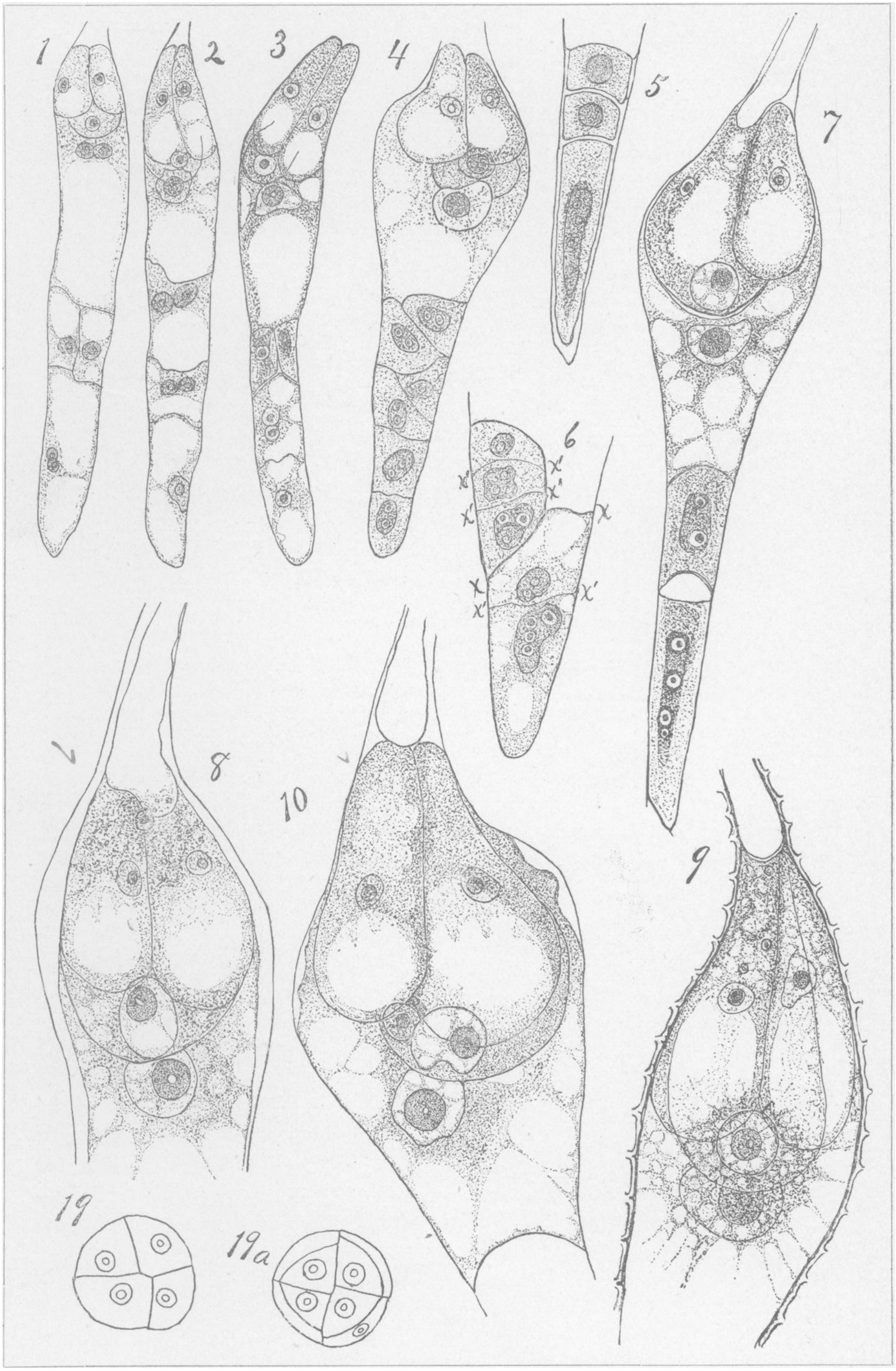
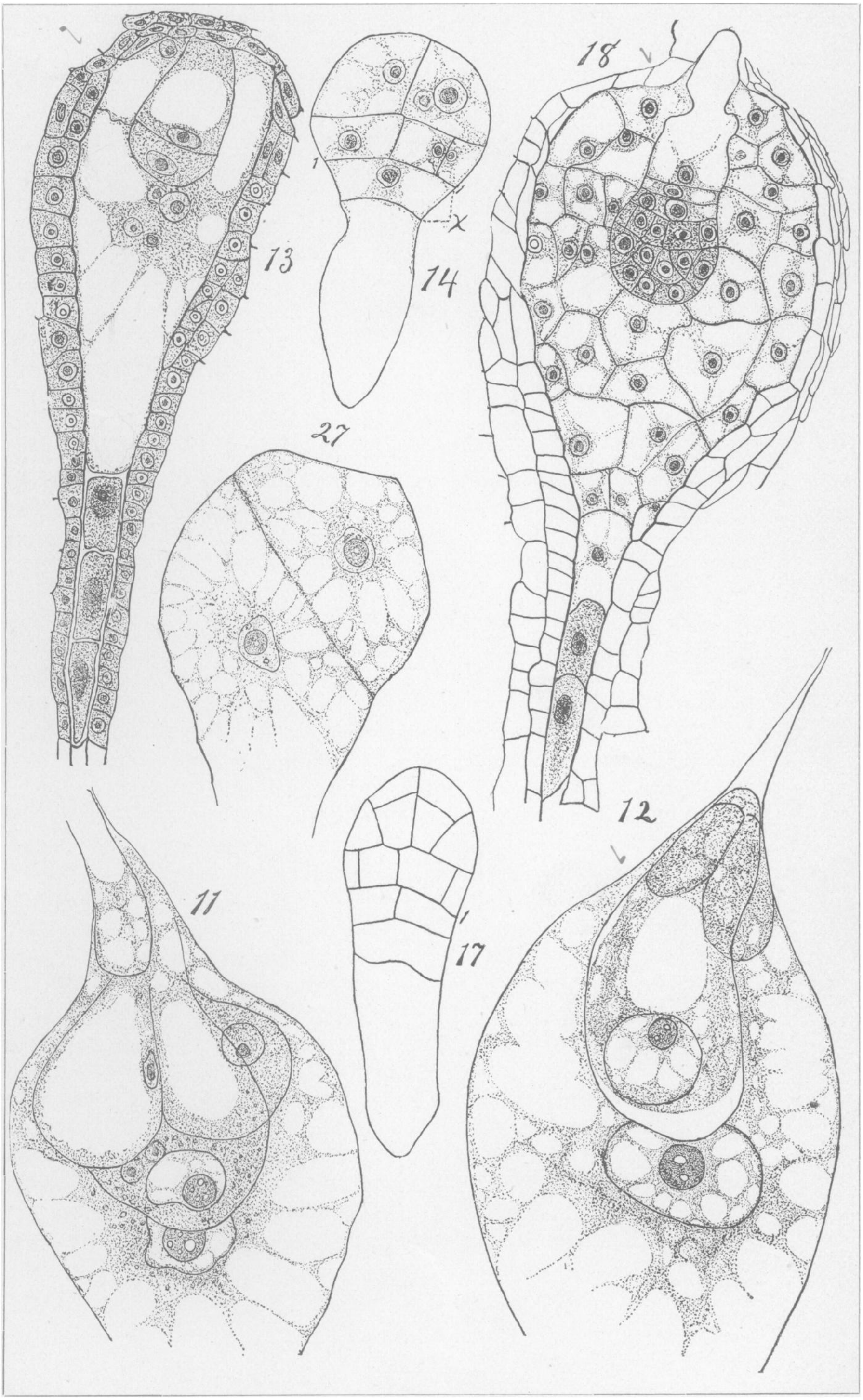


MOTTIER on SENECIO.



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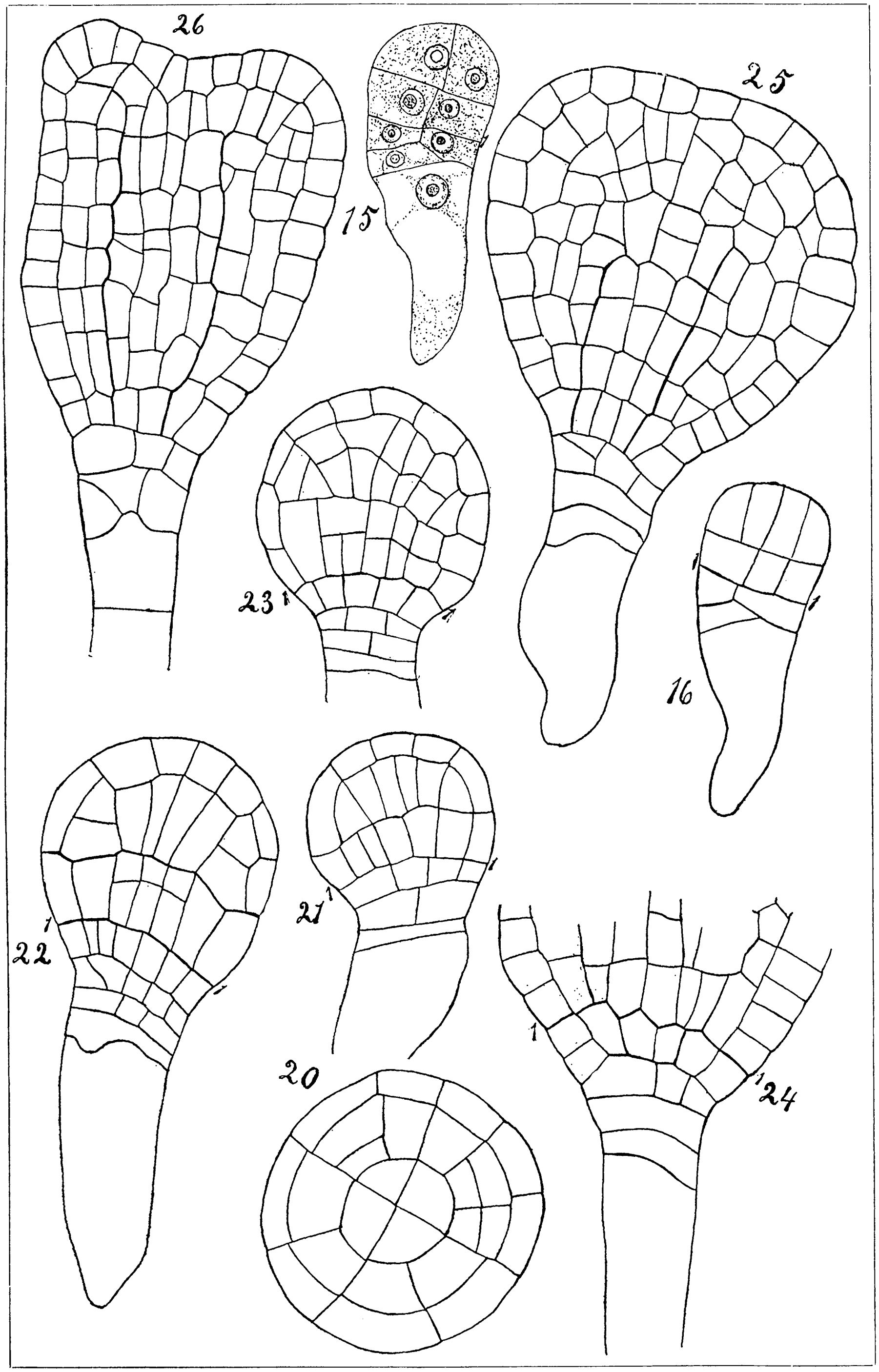

MOTTIER on SENECIO.

BOTANICAL GAZETTE

JULY, 1893.

On the embryo-sac and embryo of Senecio aureus L.

DAVID M. MOTTIER.

WITH PLATES XXVII–XXIX.

We are made familiar with the structure and development of the embryo-sac and the process of fertilization in the angiosperms by Dr. Eduard Strasburger in his masterly works, "Angiospermen und Gymnospermen," "Zellbildung und Zelltheilung," and "Theorie der Zeugung." Of the great number of plants taken as illustrative types in only one of the Compositæ are the details of the development of the embryo-sac given, namely, *Senecio vulgaris.* The Compositæ, and, it may be said, the dicotyledons in general, present many difficulties in the study of these processes.

I have observed, however, that *Senecio aureus* L., a very common native American species, is a very favorable object for the study of the embryo-sac and the early stages in the development of the embryo. Work upon this plant was undertaken chiefly for the purpose of comparison with that which obtains in some of the lower dicotyledons and monocotyledons and to see whether the process here differed in any way from that of the allied species, Senecio vulgaris, according to the account given by Strasburger.

According to our present state of knowledge the typical seven-celled embryo-sac is a structure that stands isolated in the plant kingdom. Whether this is the same for all angiosperms is not known, and, if any variation from the type exists, it is highly probable that it occurs in some of the lowest dicotyledons or monocotyledons. Unfortunately, however, in none of the lowest of those forms is the development of the embryo-sac known, and a study of this process in the lowest forms of the above named groups is beyond question necessary.

Since my results agree closely with those of Strasburger upon *Senecio vulgaris* a brief *résumé* of the latter may be for convenience given here.[1]

As will be indicated below, I am here concerned only with the nearly mature and mature embryo-sac, and such facts only as pertain to it will be mentioned. In the nearly mature embryo-sac the two synergidæ occupy the entire forward pointed end of the embryo-sac. Under these lies the egg, occupying usually the entire diameter of the embryo-sac. The antipodal cells completely fill the hinder end of the embryo-sac. They lie in a longitudinal row, or two above and one below. The lower antipodal cell gives rise to a large hinder vacuole as a cell lumen. Its nucleus lies in the protoplasm lining the wall, at about one-half the height of the cell lumen. The two nuclei given off to the inner part of the embryo-sac approach each other quickly to unite just as the embryo-sac approaches maturity. When this state of maturity is reached the embryo-sac swells considerably at its middle part. The synergidæ have now rounded themselves off somewhat at the forward end, and appear here strongly refractive. Their nuclei lie in the hinder third. By the swelling of the embryo-sac, the egg has become free at its hinder part. The lowest antipodal cell usually divides once before the mature state is reached, so that there are now four antipodal cells. Frequently, however, only the nucleus divides without being followed by a cell division.

The embryo-sac.

In preparing the material for this work heads of flowers were gathered in the stage of development desired, halved and treated for about twelve hours (usually over night) in a one per cent. aqueous solution of chromic acid. After thorough washing, they were gradually brought into ninety-five per cent. alcohol. The material was stained *in toto* with alum cochineal, imbedded (through xylol) in paraffin and sectioned on a Minot microtome. The sections were counter-stained on the slide and mounted in balsam. In this way serial sections were made of a large number of florets, and not infrequently were several stages of the young embryo obtained upon a single slide as well as mature embryo-sacs.. We are concerned here with the mature embryo-sacs, and with that stage in the development just before the nuclei given off to the interior, unite to form the endosperm nucleus. The earlier stages in the development observed agree with that which obtains in Senecio vulgaris according to Strasburger and will not be repeated here.

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[1] Angiospermen und Gymnospermen, 1879, pp. 9, 10, 11. Zellbildung und Zelltheilung, dritte Auflage, 1880. pp. 42, 43.

The two synergidae and egg-cell occupy the somewhat anterior pointed end of the embryo-sac (figs. 2, 3, 8, 9.). The synergidæ are somewhat pear-shaped, being narrower at the anterior end, where they are also rounded. In all cases observed the anterior ends of the synergidæ never appeared refractive, but filled with granular protoplasm which stained only slightly with alum cochineal, but stained readily with Bismarck brown. The posterior part of each of the synergidæ is occupied by a large vacuole which reaches fully half the length of the cell and probably extends farther forward than it seems. The vacuole does not take up the entire posterior part of the cell, but a delicate layer of protoplasm forms an inner lining of the cell. The nuclei lie imbedded in this protoplasmic lining about midway between the anterior and posterior ends. In no case were they observed in the posterior third as Strasburger states for Senecio vulgaris.

The egg-cell is similar in form to the synergidæ, though inserted a little lower, the posterior part occupying, in the many cases observed the entire diameter of the embryo-sac. The protoplasm is accumulated in the posterior end in which is imbedded the egg-nucleus, while the vacuole is in the anterior end. Thus in the egg-apparatus there is a sort of equilibrium maintained in the distribution of the protoplasm. The nucleus has a large nucleolus which stains so deeply with alum cochineal as to appear a homogeneous red, except there is invariably present from one to several highly refractive bodies resembling drops of oil. This may be due to the reagents used in preparing the tissue for sectioning and not to normal products of the nucleolus. Surrounding the nucleolus is a zone of slightly stained protoplasm, and finally the nuclear membrane which appears with great clearness. The nucleus is usually spherical though frequently compressed on one side, due probably to contraction caused by reagents (fig. 10). In nearly all preparations there was no shrinkage whatever.

When the embryo-sac is mature it swells considerably at its middle, so that the egg-apparatus is free behind.

The antipodal cells occupy the entire posterior end of the embryo-sac, which is narrow and always remains so (figs. 5, 7, 13). As in Senecio vulgaris, they lie in a longitudinal row (fig. 5), or one below and two above (figs. 1, 3); but I find here a much greater variation in the number of cells than Strasburger figures for Senecio vulgaris. In several instances only two cells were present (fig. 7), separated by a much swollen wall. The lower cell is longer than the upper and the nucleus is greatly lengthened in the direction of the axis of the embryo-sac; it contains several nucleoli and may have arisen from the fusion of two nuclei. Fig. 3 shows an embryo-sac in which the lower antipodal cell has divided, and in the upper one of these the nucleus has doubled. The doubling of the nuclei in the antipodal cells is, however, a frequent occurrence. In fig. 4 it will be seen that each antipodal cell has divided, making six in all. A curious condition of things is shown in fig. 6. The wall, x, was well developed, but the others, x', x', were extremely delicate.

In many cases the walls separating the antipodal cells were slightly swollen (fig. 5). These facts seem to indicate that the antipodal cells represent a structure that shows a tendency toward further development, suggesting a much reduced prothallium or rudimentary structure of some kind, and a comparison of it with a prothallium of the vascular cryptogams seems reasonable.

The fusion of the two nuclei to form the endosperm nucleus takes place after the formation of the egg apparatus and antipodal cells. In no case were the antipodal cells observed lying free without cell walls at the time when the nuclei were about to unite to form the endosperm nucleus; the walls were always well developed at this stage.

Of the two nuclei given off into the cavity of the embryo-sac, the one which comes from the antipodal end traverses the greater distance and meets its fellow close to the egg-cell where they unite (fig. 1). The endosperm nucleus invariably lies very near the egg, apparently touching it in many cases (figs. 4, 8, 9, 10). Its structure is similar to that of the egg nucleus, except it is much larger in every respect. It is surrounded by rather dense granular protoplasm from which radiate delicate threads connecting with the very delicate layer of protoplasm lining the cavity of the sac. In this particular fig. 9 is the most interesting. Here a very beautiful net-work of protoplasm seems to radiate from the region of the egg nucleus, though between it and the observer, almost obscuring the endosperm nucleus lying beneath.

Fertilization.

Senecio aureus is by no means a very favorable object for the study of the process of fertilization. As is well known, the dicotyledons as a rule, present here many difficulties. Either the ovules are opaque, necessitating sectioning, or the nuclei in the pollen tube as well as the tube itself are extremely small. In Senecio aureus and the Compositæ in general both of these difficulties confront the observer. However, by the aid of a 2^{mm} oil immersion I was enabled to demonstrate the presence of the pollen tube in the micropyle and the generative nucleus after it had entered the egg-apparatus. In no case was the presence of a pollen tube in the style or any part of the ovary wall observed, consequently the exact path followed by it was not determined. The end of the tube was seen just as it had reached the anterior ends of the synergidæ (figs. 7, 8, 9, 10). Its membrane is extremely delicate and the tube collapses soon after the contents have left it. The contents now spread out upon the anterior ends of the synergidæ, make them appear more densely granular (figs. 8, 9). The generative nucleus as it leaves the pollen tube, appears as a very small and slightly stained mass of nuclear substance (fig. 8). By the time it has reached the egg nucleus, however, it has increased considerably in size (fig. 10), having been nourished by the contents of the egg apparatus. In the preparation represented in fig. 9, the presence of a pollen tube was quite evident, the anterior ends of the synergidæ densely granular, but no definite nucleus could be seen. Two small bodies more densely stained than the rest are present, which take on the character of nuclear substance.

The wall of the micropyle just in front of the synergidæ stained a homogeneous brown (not shown in the figures), suggesting strongly the presence of a mucilaginous substance, which in all probability is secreted by the synergidæ. In fig. 10 the generative nucleus is seen lying close to the egg-nucleus. In fig. 11, two, though smaller, nuclei are seen. Even at this stage in the process, the synergidæ seemed very little changed, except their membranes were extremely delicate and almost indistinguishable. In fig. 11 the synergidæ on the left showed disorganization, the nucleus being smaller and vacuole larger.

Development of the embryo.

The fertilized egg, oospore, increases in size, becomes slightly elongated, and develops a more definite membrane (fig. 12). The posterior part (that directed toward the micropyle) now protrudes slightly into the micropyle to serve as an organ of attachment. The nucleus increases now greatly in size as does the endosperm nucleus also. The synergidæ are almost entirely absorbed; their remains are shown in the figure. The oospore now divides near its upper end (that directed away from the micropyle) by a transverse wall into a terminal hemispherical cell and a basal cylindrical cell (fig. 13). The terminal cell forms the greater part of the future embryo, while the basal cell forms the suspensor and a part of the embryo. This differs from that which obtains in *Capsella*[2] in that the oospore does not elongate into a tube which first divides by a number of cross walls to form the suspensor. Here the suspensor remains shorter; it is composed of fewer cells and the divisions take place later. At this stage of development (fig. 13), several free nuclei have arisen in the cavity of the embryo-sac from the division of the endosperm nucleus.

This terminal cell of the embryo, after further increase in size, divides into halves by a longitudinal wall. This is followed by a second longitudinal wall at right angles to the first, as will be seen in a cross section of the same at a similar stage of development (fig. 19). A third wall, transverse, follows at right angles to the first two. The terminal cell has now divided into eight cells, which may be compared to the octants of a sphere. From the upper half of the embryo which is cut off by the transverse wall, proceeds subsequently the epicotyledonary (plumule and cotyledons) portion of the embryo, and from the lower, the hypocotyledonary (radicle) portion. At this stage of development (fig. 14) a cell is cut off from the upper end of the suspensor by a transverse wall. This cell, *x*, subsequently contributes to the formation of the periblem of the root, the root cap and suspensor. The three walls mentioned above which divide the original terminal cell of the embryo into octants follow each other rapidly; for in different flowers of the same head, embryos as represented in fig. 13 were very frequently found along with those developed as far as shown in fig. 16 or farther. The stage figured in fig. 14 was rarely met with.

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[2] Goebel: Outlines of Classification and Special Morphology, English translation, 1887, pp. 396, 397, 398.

The usual form of the embryo at this stage of development is that which is figured in figs. 17, 18, the figures representing longitudinal sections.

Each of the four upper cells of the embryo is now divided into two by anticlinal walls (fig. 16). Immediately following this each cell of the embryo is separated into an inner and outer cell by its periclinal wall (figs. 18, 21). The outer row of cells is the dermatogen or young epidermis; its cells divide henceforward only by walls at right angles to the outer surface, i. e., anticlinal walls, no periclinal walls being formed. The inner cells are the initial elements of the periblem and plerome, which are very early distinguishable from each other. This may be plainly seen in fig. 22, and in fig. 20, which is a cross section of a young embryo. The cells of the periblem and plerome now divide by both longitudinal and transverse walls, the divisions being quite regular for a time (figs. 22, 23), but as the embryo increases in size they become less regular (fig. 25).

The cell divisions which take place in the cell *x*, fig. 14, do not seem to follow with as great regularity as in Capsella. It divides once or twice by transverse walls (figs. 18, 21, 23, 24), and the cells thus formed divide further by longitudinal walls, though with no great regularity (figs. 22, 24). Whether any cell or cells are cut off from the upper part of the large cell of the suspensor could not be determined, as the nucleus was not seen in process of division. However, as above stated, it contributes to both embryo and suspensor.

The suspensor consists of few cells, usually three or four, the lower one remaining large and cylindrical, and projecting slightly into the micropyle (figs. 18, 22, 25). In fig. 26 the first appearance of the cotyledons is seen; the limits of periblem and plerome are indicated by heavy lines. Thus at this stage of development those parts which are to become the root, stem and cotyledons are quite apparent (figs. 25, 26), even as early in the development as represented in figs. 21, 22. Further development of the embryo was not followed.

The endosperm.

As stated in the foregoing, several free nuclei appear in the cavity of the embryo-sac when the first wall is formed in the embryo. Very soon, however, cell formation takes place, and the cavity of the embryo-sac is entirely filled with endosperm (fig. 18). In some cases the embryo was further developed than others before cell formation took place in the endosperm. The process of cell building here is that of the Capsella type.[3] This is not a favorable object for the study of the details in the process of cell-formation. I was not able to make out the "Verbindungsfäden" of Strasburger.[4] Fig. 27 shows two endosperm cells that occupied the whole width of the embryo-sac in which was the embryo, fig. 16. Figs. 27 and 16 were taken from consecutive sections. Around each nucleus (fig. 27) whose membrane is somewhat contracted, is an accumulation of protoplasm from which radiate delicate protoplasmic threads.

The endosperm cells are relatively large and not very rich in protoplasm. The layer of cells forming the wall of the embryo-sac, which is the modified adjacent part of the integument of the ovule, is rich in protoplasm, nuclei and contents staining densely with cochineal stain. The neighboring cells of the integument soon begin to disorganize (fig. 18).

Very noticeable is the fact that here the antipodal cells are not absorbed during the formation of the endosperm, but persist throughout. They were in the perfectly normal condition even when the embryo had reached the size figured in fig. 26, and the endosperm had been somewhat absorbed. The end of the embryo-sac occupied by them remains narrow, but widens abruptly above them (fig. 18).

Here the behavior of the antipodal cells seems very peculiar. Just what they represent in the angiosperm embryo-sac is still a mystery, and it seems to me that at present the facts are insufficient to justify speculation. We must wait, at least, until the development of the embryo-sac is known in the lowest forms of the angiosperms.

University of Indiana, Bloomington.

EXPLANATION OF PLATES XXVII–XXIX.

Figs, 8, 9, 10, 11, 12, 20, ×560 diam. Figs. 13, 18, ×280 diam.; all the rest ×405 diam.—Fig. 1. Embryo-sac just before the formation of the endosperm nucleus.—Figs. 2, 3. Embryo-sacs just before the flower opens, measuring .152^{mm} in length.—Fig. 4. Antipodal cells divided, the two upper by oblique walls.—Fig. 5. Elongated nucleus of the lower antipodal cell.—Fig. 6. Peculiar condition of antipodal cells; the wall x well developed; x', x', very delicate.—Fig. 7. Embryo-sac at the time of fertilization, .216^{mm} long by .048^{mm} wide.—Figs. 8, 11. Upper part of embryo-sac showing egg-apparatus, endosperm nucleus and pollen tube.—Fig. 12. Fertilized egg; synergidae disappearing.—Fig. 13. Embryo-sac with two-celled embryo.—Fig. 18. Embryo further developed, surrounded by endosperm tissue. Figs.—14, 17. Embryos in different stages of development; 1—1 primary transverse wall.—Figs. 19-20. Transverse section of upper end of young embryo; in 19a and 20 the four cells forming the inner circle are the plerome; the next outer row the periblem; and in 20 the outermost row the dermatogen.—Figs. 21-26, longitudinal sections of older stages of the embryo; in figs. 25 and 26 the heavier lines indicate the boundary between plerome and periblem.—Fig. 27, two endosperm cells.

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[3] Zellbildung und Zelltheilung, dritte Auflage, 1889, p. 11.

[4] Strasburger: Ueber Befruchtung und Zelltheilung, 1878, p. 71.

Descriptions of new species of Uredineæ and Ustilagineæ, with remarks on some other species. I.

P. DIETEL.

The following described species of fungi, principally Uredineæ, have been collected by Mr. E. W. D. Holway and some other collectors in California and several other portions of the United States. Three other new species, namely, *Uromyces aureus* Diet. and Holw., *Puccinia Holwayi* Diet., and *Puccinia Delphinii* Diet. and Holw., have already been published in Hedwigia, XXXII (1893). 29, 30.

Ustilago Holwayi Diet. n. sp.—Spore masses black-brown, pulverulent, destroying the whole inflorescence. Spores subglobose or obovate, brown, with large warts, 8–13μ in diameter.

On *Hordeum pratense.* Camp Badger, Calif., July, 1892, leg. *Holway.*

From the similar *Ustilago Lorentziana* Thüm. (Mycotheca univ. no. 1711) this differs, as an examination has shown, by the shape of the epispore.

Puccinia rufescens Diet. and Holw. n. sp.—Spots none. Æcidia forming loose and irregular groups, or isolated on both sides of the leaves. Pseudoperidia hemispherical, with decaying edges, composed of oblong, loosely aggregated cells. Æcidiospores mostly ovoid or obovate, with a light brownish membrane, containing orange red protoplasmic contents,